EVOLUTIONARY SYSTEMATICS AND PARAPHYLY: INTRODUCTION[1]

Tod F. Stuessy[2] *and Elvira Hörandl*[3]

ABSTRACT

Phylogenetic systematics, especially involving molecular data, has had a remarkable impact on systematic biology. Numerous tree-building computer programs exist for the reconstruction of phylogenies, and many packages are available for analysis of population genetic data for estimating genetic divergence within and among populations. These advances have come about through the joining of statistical algorithms, computer programs, and DNA base-pair sequence and fragment data. Deeper genomic data are on the horizon for use with similar questions, and the next several years will witness many spectacular genetic advances. While great progress is being made on analytical approaches with molecular data in systematics, the use of the results of these analyses in biological classification has solidified into a dogmatic view, which has impeded further progress. Emphasis still remains on using only synapomorphies, even single characters, for delimitation of groups, on insisting that sister groups should have the same rank, and admitting only holophyletic (= monophyletic s. str.) groups. Evolutionary divergence within lineages and reticulate evolution are often ignored. As a result of these processes, paraphyletic groups, i.e., monophyletic groups that do not contain all descendants from a common ancestor, are often rejected. Evolutionary systematics takes the processes of descent and modification into consideration for reconstructing phylogenetic relationships involving many dimensions. This symposium presents various approaches for recognizing cladogenetic, anagenetic, and reticulate evolution in different organisms, which help reveal micro- and macro-evolutionary processes. Controversy still exists regarding how taxonomists should incorporate the diversity of evolutionary patterns and processes into biological classification. Case studies demonstrate that purely phylogenetic (cladistic) concepts of classification are unsatisfactory in cases of non-hierarchical relationships. Contributions also deal with the controversial question of recognition of paraphyletic groups in classification.

Key words: Cladistics, classification, divergence, evolution, patristics.

Biological classification has a complex history. In pre-Linnaean and Linnaean times, classification was relatively simple, in that one sought differentiating characters that were chosen by God to distinguish all created organisms. The development of natural systems of classification in the 18th century emphasized the importance of using constellations of characters together for maximum predictive quality of classifications. In the 19th century, Darwin (1859) taught that groups established through natural classification have derived by descent and modification from common ancestors. This perspective served as a basis for evolutionary classification until appearance of quantitative approaches in the last half of the 20th century.

Beginning in the late 1950s, dissatisfaction with intuitive approaches to science, including classification, led to development of more precise methods. Discovery of the molecular structure of DNA (Watson & Crick, 1953), the basis of heredity, suggested that many biological phenomena might be interpretable in quantitative terms. Phenetics, or the assessment of overall similarity using numerical methods, developed as the first attempt at quantitative classification (Michener & Sokal, 1957; Sneath, 1957; Sokal & Sneath, 1963). To achieve this end, evolutionary assumptions were minimized, which initially proved to be intellectually stimulating, but later was regarded as insufficient, as basic realities of the organic world were ignored. Into this challenge came cladistics (Hennig, 1966), which attempted to reconstruct branching patterns of evolution (or phylogeny). To successfully provide a means of ease of calculation and convenient inter-conversion between diagram (cladogram) and resultant classification, cladistics ignored divergence within lineages. Despite this limitation, cladistic analysis has become an important tool of evolutionary analysis in many areas of biology, along with the re-employment of phenetic algorithms that are more efficient when analyzing large sets of molecular data.

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[2] Department of Systematic and Evolutionary Botany, Biodiversity Center, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. Present address: Herbarium and Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 1315 Kinnear Road, Columbus, Ohio 43212, U.S.A. stuessy.1@osu.edu.

[3] Department of Systematics, Biodiversity and Evolution of Plants (with Herbarium), Albrecht-von-Haller-Institute for Plant Sciences, Georg-August-University of Göttingen, 37073 Göttingen, Germany. elvira.hoerandl@biologie.uni-goettingen.de.

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During developments of phylogenetic analysis over the past 30 years, however, a number of workers have suggested that despite positive contributions, cladistic *classification* is too narrow because it does not reflect full dimensions of phylogeny. Quantitative evolutionary classification, therefore, developed in the 1980s. This involved adding quantitative values to character divergence within lineages, to be combined with the dichotomous patterns of relationship determined via cladistic analysis. In a sense this represented returning to evolutionary classification prior to phenetics and cladistics, but now also in a completely quantitative framework. Several approaches have been developed, such as convex phenetics (Estabrook, 1986), addition of cladistic and patristic distances in a single data matrix, followed by appropriate clustering (Stuessy, 1987), patrocladistics (Stuessy & König, 2006), etc. Although these methods for quantitative evolutionary classification have not received widespread use, they have been sufficient to indicate that other aspects of phylogeny can, indeed, be incorporated quantitatively into biological classification. That is, there is certainly no need to be limited only by branching pattern information. If representation of phylogeny is really the goal of biological classification, then we should aggressively seek quantitative means of obtaining more, rather than be satisfied with fewer, dimensions of phylogeny.

The Meaning of Paraphyly

Paraphyly is not a contagious disease. It is also not an evolutionary grade. Paraphyly is an evolutionary stage of monophyletic taxa (s.l.) that needs to be taken into account for purposes of biological classification. Arguments for this perspective and suggestions on how this should be done successfully have formed the principal focus of the present symposium.

The main area of conflict between cladistic and evolutionary classification is the insistence of the former on strict holophyly. A holophyletic group is one that includes the immediate ancestor and *all* its descendents, independent of whatever divergence occurs within each of the derivative lineages (Ashlock, 1971). A paraphyletic group is one that derives from a common ancestor but that does not contain all its descendents (Hennig, 1966). For example, a new species that buds off from a parental set of populations forms a new holophyletic species, but the progenitor then becomes paraphyletic, and hence, unacceptable following cladistic conventions.

After Darwin (1859), all groups in classification were regarded as being evolutionary units, having been derived from the evolutionary process. All legitimate groups in classification (i.e., the taxa placed into classes of the hierarchy) were monophyletic. Non-monophyletic groups, that is, those that are polyphyletic, deriving from two or more independent ancestors, were unacceptable, then as now. This perspective endured successfully until the rise of cladistics in the 1960s, which coincides most conspicuously with the appearance of the English version of Hennig's book (1966). To provide a *convenience* of transformation of a branching pattern into a hierarchical classification and the reverse, that is, to have no ambiguity, Hennig narrowed the concept of monophyly to refer to an ancestor and all its descendents. This new definition, however, excluded groups that derive from a common ancestor but that do not include all the descendents. Hennig named these latter groups paraphyletic and excluded them from acceptable classification. Because this created a significant deviation from previous perspectives, Ashlock (1971) recommended calling this more narrow perspective holophyly and regarded both it and paraphyly as forms of monophyly s.l. We advocate this perspective (Hörandl & Stuessy, 2010; Stuessy & Hörandl, 2014), which is also maintained in many papers of this present symposium.

Paraphyly as Part of the Evolutionary Process

Paraphyly, therefore, is very much a part of the evolutionary process (Hörandl, 2007). Essentially, paraphyly and holophyly are alternating conditions that cycle forward and change over many generations (Hörandl, 2006; Hörandl & Stuessy, 2010). A newly originated species usually is holophyletic (= monophyletic s. str.), but depending upon its mode of origin, it can leave the progenitor holophyletic or paraphyletic. With geographic allopatric speciation, two sets of populations diverge equally (or nearly so) from each other, resulting in extinction of the progenitor in the process. In a pattern sense, the entire group remains holophyletic because divergence is symmetrical. Another case would be adaptive radiation, common in oceanic islands, whereby divergence in many different geographical and ecological directions occurs simultaneously, all equidistant in divergence from the progenitor, which in the process ceases to exist. Conditions in which the progenitor is rendered paraphyletic, whereby divergence is asymmetrical, occur with several types of progenitor-derivative speciation (Crawford, 2010). One common example involves budding of new populations that continue to accrue reproductive isolation and speciation, leaving the parental populations virtually intact (Hörandl & Stuessy, 2010). As emphasized by Stuessy et al. (2014), this type of progenitor-derivative speciation exists within oceanic islands, whereby colonizers from large genera disperse successfully to a new island environment and there evolve into one or more groups of new distinctive endemic species, to such an extent that they may be regarded as distinct genera. Another type of evolution that results in paraphyletic parental taxa is reticulate speciation, i.e., allopolyploidy, whereby both parents involved with the initial hybridization become paraphyletic after formation of the successful daughter polyploid. Several reviews have estimated high levels of paraphyly at the specific level (e.g., Rieseberg & Brouillet, 1994; Funk & Omland, 2003).

Objectives of the Symposium

Interest in aspects of cladistics, evolutionary systematics, and paraphyly led to the holding of a symposium on the topic "Evolutionary systematics and paraphyly" during the International Botanical Congress, Melbourne, Australia, 28 July 2011. The objective was to present different perspectives toward moving forward from simple cladistic classifications to models that contain more phylogenetic information, all in a quantitative framework.

It is very appropriate at this point in time to consider seriously these issues. One segment of our systematics community is already convinced that phylogenetic analysis, using mainly molecular data, with interpretation using cladistic rules of classification, is the solid way for information structuring now and into the foreseeable future. Other workers in our community, however, are very supportive of phylogenetic analysis using molecular data, but find that strict cladistic classification, with reliance on holophyly, is not the appropriate information structure to serve societal needs either now or certainly not into the future. More progress needs to be achieved, as has always been the case in the development of our field. As one example, some workers are highly supportive of the Angiosperm Phylogeny Group (APG) classification of angiosperms (APG, 1998, 2003, 2009), based largely on DNA data and phylogenetic analysis, *and* interpreted in the context of cladistic rules of classification. Although this initiative, in general, represents a clear advance in phylogenetic synthesis for the entire botanical community, some of the results presented distorted information content regarding certain families. Plantaginaceae, for example, now contain genera with virtually no morphological resemblance to the genus *Plantago* L., and not surprisingly, some workers find it difficult to accept this approach (Brummitt, 2014).

The papers in this symposium reflect different interests in evolutionary systematics, with investigations focusing on the nature of species at the populational level (Lockhart et al., 2014), the problem of holophyly and paraphyly and conservation impact on recognition of endemic genera in oceanic islands (Stuessy et al., 2014), the utility of paraphyly in addressing specific and generic concepts (Ehrendorfer et al., 2014; George, 2014; Hörandl, 2014), methods for finding support values for phylogenetic lineages (Zander, 2014), and issues relating to holophyly and paraphyly among angiosperm (dicot) families (Brummitt, 2014).

We recognize that this one symposium will not solve all issues relating to biological classification. We strongly believe, however, that the time has come to look critically at simple cladistic classification couched in a narrow evolutionary context and expand this into quantitative evolutionary approaches that capture more phylogenetic information. This is the only way to provide a more information-rich system with higher predictive value for biology and society as a whole. This was the spirit of the symposium.

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